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Growth and Photosynthetic Responses of Wheat Plants Grown in Space[1]

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Growth and photosynthesis of wheat (*Triticum aestivum* L. cv Super Dwarf) plants grown onboard the space shuttle Discovery for 10 d were examined. Compared to ground control plants, the shoot fresh weight of space-grown seedlings decreased by 25%. Postflight measurements of the O_2 evolution/photosynthetic photon flux density response curves of leaf samples revealed that the CO_2-saturated photosynthetic rate at saturating light intensities in space-grown plants declined 25% relative to the rate in ground control plants. The relative quantum yield of CO_2-saturated photosynthetic O_2 evolution measured at limiting light intensities was not significantly affected. In space-grown plants, the light compensation point of the leaves increased by 33%, which likely was due to an increase (27%) in leaf dark-respiration rates. Related experiments with thylakoids isolated from space-grown plants showed that the light-saturated photosynthetic electron transport rate from H_2O through photosystems II and I was reduced by 28%. These results demonstrate that photosynthetic functions are affected by the microgravity environment.

Prolonged missions and colonization of space by humans will require a reliable life-support system. Physical-chemical systems with biological components, each with distinct advantages, have been proposed (Schwartzkopf, 1993). Physical systems can be accurately defined, controlled, and modeled but can be subject to mechanical failures. Biological or bioregenerative life-support systems are somewhat less defined in terms of component processes but have a resiliency that the physical systems do not. Therefore, it is essential to know the role of microgravity on plant growth, development, and reproduction.

In recent years there has been a rapid growth in our knowledge of the role of gravity in plant growth and development resulting from the biological experiments carried on the Mir space station and in the shuttle middeck lockers (for reviews, see Halstead and Dutcher, 1987; Halstead and Scott, 1990; Dutcher et al., 1994). One complete life cycle was achieved in 1982, when *Arabidopsis thaliana* plants grew from seed to seed, although plant growth was reduced and there were only a few seeds in the siliques. The seeds were less vigorous and were abnormal (Merkys and Laurinavichius, 1983). Siliques of *A. thaliana* plants flown in the U.S. space shuttle (STS-54) contained empty, shrunken ovules, although 80% of the pollen grains were viable (Kuang et al., 1994). Preliminary studies revealed chromosome breakage and bridge formation in space-grown oat and sunflower seedlings (Krikorian and O'Connor, 1984; Levine and Krikorian, 1992).

Gravity is believed to be perceived by starch grains present in amyloplasts. Leaves of pea plants grown aboard Salyut-7 lacked starch reserves and contained very few grains (Abilov et al., 1986; Aliyev et al., 1987). Johnson and Tibbitts (1968) found significantly lower starch content in leaves of pepper plants grown aboard Biosatellite II. Other examples of reduced starch concentration or starch volume include Arabidopsis (Laurinavichius et al., 1986; Brown et al., 1993), *Lepidium* roots (Volkmann et al., 1986), and maize root columella cells (Moore et al., 1987).

Swollen mitochondria with an electron-dense matrix and well-developed cristae structure were seen in Arabidopsis (Kordyum et al., 1983). Sweet clover seedlings grown in the fluid-processing apparatus fitted with gas-permeable membranes aboard the U.S. space shuttle (STS-60) produced CO_2 at a level three times the ambient level (Gallegos et al., 1994).

There are conflicting reports about the Chl content of space-grown higher plants. Abilov et al. (1986) and Aliyev et al. (1987) reported an increase in Chl content of space-grown pea plants. In contrast, Laurinavichius et al. (1986) observed a decrease in Chl content in space-grown pea plants. The Chl and carotenoid content were reduced in maize plants grown on Mir for 19 d (Rumyantseva et al., 1990).

Total Chl and carotenoid content of *Chlorella vulgaris* grown on the space station Mir was reduced by 35 to 50%. However, the algal cells partially recovered from the space-flight-induced damage within 24 h after landing (Meleshko et al., 1991). Space-grown *Chlorella* cells showed a decrease in the number and size of starch grains in chloroplasts and

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Abbreviations: DCIP, 2,6-dichlorophenol indophenol; EDT, eastern daylight time; MV, methyl viologen; OES, orbiter environmental simulator; PD, *p*-phenylenediamine; PGC, plant growth chambers; PGU, plant growth unit.

an increase in the size of the cell vacuole (Popova et al., 1989). Postflight ultrastructural studies of *C. vulgaris* cells flown on Mir more than 30 d on a solid agar medium showed changes in the plastid membrane systems, including the appearance of vesicles of various sizes in the stroma, outgrowths from the plastids reaching the plasma membrane, and an increase in the volume of mitochondria and their cristae (Sytnik et al., 1992).

Ultimately, the bioregenerative life support system and plant growth and development depend on photosynthesis, through which plants convert radiant light energy to chemical energy to produce food and oxygen and remove CO_2. The oxygenic photosynthetic mechanism of plants has evolved under the constant force of gravity. To understand the role of microgravity on plant growth and development and to determine if a bioregenerative life support system can be sustained in space, it is essential to determine if the photosynthetic process is affected in the space/microgravity environment.

Although limited, there is some evidence of structural perturbation of the photosynthetic apparatus in space-grown plants. Chloroplasts of space-grown pea plants showed disintegration of grana, disorientation of stromal lamellae, and shrinkage of the membranes constituting the grana stacks (Abilov et al., 1986; Laurinavichius et al., 1986; Aliyev et al., 1987). However, there have been no studies on the effect of spaceflight on photosynthesis.

Therefore, the objectives of this initial study were to characterize several critical photosynthetic parameters in leaves of wheat (*Triticum aestivum* L.) plants that had grown in space and compare these to synchronous, ground control plants. Because in-flight manipulation by the shuttle crew was not possible, harvest of plant parts and photosynthetic measurements were done postflight.

MATERIALS AND METHODS

Hardware

Plants were grown in the PGU, a plant growth chamber designed to fit within a middeck locker of the space shuttle. The PGU contains six PGCs, which have self-contained sealed atmospheres (Krikorian and Levine, 1991). Each PGC consists of an aluminum alloy base and a transparent polycarbonate lid that fit together over a silicone rubber gasket. Lighting for plant growth was provided by Vita-Lite (ILC Technologies, Sunnyvale, CA) fluorescent lamps having a PPFD of 50 to 60 μmol m^{-2} s^{-1}.

Plant Culture

Wheat (*Triticum aestivum* L. cv USU Super Dwarf) seeds were sterilized in 2.6% (w/v) sodium hypochlorite plus 1% (w/v) Triton-X 100 for 20 min, rinsed four times in sterile water, and then placed into individual germination jars containing one-eighth-strength Hoagland nutrient solution supplemented with 0.5% (w/v) Suc solidified with 0.7% (w/v) agar. A vernalization treatment was needed for adequate germination of the Super Dwarf cultivar. Jars were maintained at 4°C in the dark for 3 d and then transferred to an illuminated 22°C chamber for 24 h. At this point (the day before shuttle liftoff), each germination jar was examined for signs of contamination and the most vigorous seedlings were chosen for placement into the PGCs. Twelve seedlings were grown in each PGC using a modification of the aseptic foam/nitex system (Levine and Krikorian, 1992). Sterile, half-strength Schenk and Hildebrandt (1972) medium supplemented with 1.5% Suc (w/v) was added to the foam (110 mL/PGC) immediately before the seedlings were inserted into the PGCs. The RH in the PGCs was 90 to 100%. CO_2 was injected (through a hole made in the foam above a gas sampling port built into the PGC base) after sealing the PGCs. The internal concentrations of CO_2 in the different PGCs used for ground control and spaceflight were 6,153 to 8,281 μL L^{-1} at the beginning of the mission, and these increased to 31,127 to 33,802 μL L^{-1} at the end of the mission. Thus, there was no significant variation in CO_2 concentration in ground control and spaceflight PGCs. The seedlings were approximately 2 d old at the time of space shuttle liftoff.

Flight

Loading of the PGCs into the PGU was completed at 1:35 PM EDT on September 11, 1993, and the PGU was installed into the middeck of the space shuttle Discovery at 6:00 PM EDT. Liftoff was at 7:45 AM EDT on September 12, 1993, at the Kennedy Space Center (Cape Canaveral, FL). The orbiter landed at the Kennedy Space Center at 3:56 AM EDT on September 22, 1993, giving a total mission elapsed time (launch to landing) of 9 d, 20 h, 11 min. Plants received continuous illumination during flight. Each plant had three leaves at the end of the mission.

Ground Controls

Synchronous ground controls using identically treated plants were performed using the OES. The OES used down-linked data to control the temperature, RH, and CO_2 concentration in an environmental growth chamber at the Kennedy Space Center. The on-orbit temperature, RH, and CO_2 profiles were used to control the OES chamber in which the PGU was placed. PGU temperatures during the space mission fluctuated primarily between 22 and 26°C, but ranged from 19.3 to 28.1°C. Light intensity within the PGU was found to be identical (50–60 μmol m^{-2} s^{-1}) in the spaceflight and ground control hardware and did not vary during the mission.

Measurement of Shoot Fresh Weight

The PGU was delivered to the life science support facility 2 h postlanding. Plants were harvested from the PGCs immediately upon receipt of the PGU and the shoot fresh weights were taken.

Photosynthetic Light Response of Leaf Discs

Leaves were removed from the shoots immediately for photosynthetic measurements. Measurements of the photosynthetic light response were done on leaf discs using a "Leaf-disc Electrode," a small, temperature-controlled leaf

chamber having a Clark-type O_2 electrode (Hansatech, King's Lynn, UK) for polarographic measurement of gas phase O_2 exchange. CO_2 (5%, v/v) from a gas tank was supplied to the chamber containing the leaf discs and was also generated within the chamber from a bicarbonate buffer (Walker, 1987). All experiments were done in saturating CO_2 to avoid diffusive CO_2 limitation and to suppress photorespiration. The light intensity was controlled by varying the electrical current to red-light-emitting diodes (660 nm). Incident PPFD at the leaf surface was measured with a quantum sensor (Skye Instruments, Llandrindod Wells, UK). The relative quantum yield of CO_2-saturated photosynthesis, defined as net μmol O_2 evolved m^{-2} leaf area s^{-1}/μmol PPFD incident on m^{-2} leaf area s^{-1}, was measured at limiting light intensities (0–80 μmol m^{-2} s^{-1}) by least-squares regression analysis.

Chloroplast Isolation

Chloroplast thylakoids were isolated from the leaves at 4°C by hand homogenization in a grinding medium consisting of 0.4 M Suc, 10 mM NaCl, and 20 mM Hepes/NaOH, pH 7.6 (Tripathy and Mohanty, 1980). The same medium was used for resuspension. Chl was extracted in 80% (v/v) acetone and determined by the method of Arnon (1949).

Electron Transport

Electron transport activity through PSII supported by PD was monitored polarographically as O_2 evolution with a Hansatech DW 2/2 O_2 electrode. The 1-mL reaction mixture consisted of 50 mM Hepes/NaOH, pH 7.5, 3 mM $MgCl_2$, 10 mM NaCl, 1 mM NH_4Cl, 1 mM $K_3Fe(CN)_6$, 1 mM PD, and chloroplasts (10 μg of Chl). Chloroplasts were illuminated with a tungsten lamp source at a PPFD of 2000 μmol m^{-2} s^{-1} (Chakraborty and Tripathy, 1992).

Electron transport through both photosystems was measured from H_2O to MV as O_2 uptake in the Hansatech DW 2/2 O_2 electrode. The assay medium (1 mL) consisted of 50 mM Hepes/NaOH, pH 7.5, 3 mM $MgCl_2$, 10 mM NaCl, 1 mM NH_4Cl, 1 mM NaN_3, 0.5 mM MV, and chloroplasts (10 μg of Chl) (Tripathy and Chakraborty, 1991).

Partial electron transport through PSI was measured polarographically as O_2 uptake (Tripathy and Chakraborty, 1991). Electron flow from PSII was blocked by DCMU; ascorbate/DCIP was used as the electron donor to PSI, and MV was used as the electron acceptor. The assay conditions were identical to those of the whole-chain assay except that 10 μM DCMU, 1 mM sodium ascorbate, and 0.1 mM DCIP were added to the 1-mL reaction mixture. Chloroplasts were illuminated as described above.

Absorption and Fluorescence Spectra of Chloroplasts

The absorption spectra of chloroplasts were recorded in a Beckman DU64 spectrophotometer. Isolated chloroplast membranes were suspended in 50 mM Hepes/NaOH, pH 7.5, 3 mM $MgCl_2$, 10 mM NaCl, and 50% (v/v) glycerol at a Chl concentration of 3 μg mL^{-1}. The absorption spectra were not corrected for absorption flattening. Room-temperature (20°C) fluorescence spectra were recorded in a Perkin-Elmer LS 50B spectrofluorometer. Chloroplasts were excited at 440 nm and the fluorescence spectra were recorded at excitation and emission slit widths of 5 nm. Chloroplasts (3 μg Chl mL^{-1}) were suspended in a medium consisting of 50 mM Hepes/NaOH, pH 7.5, 3 mM $MgCl_2$, and 10 mM NaCl.

RESULTS

Seedling Shoot Fresh Weight

Average shoot fresh weight was taken from a population of 18 seedlings. The average shoot fresh weight of space-grown wheat seedlings was 115.4 ± 8 mg. This value was 25% lower than that of ground controls, which was 153.4 ± 11 mg.

Photosynthetic Light Response

The measurement of CO_2-saturated O_2 evolution by the leaf discs at increasing PPFD revealed that net O_2 evolution by space-grown plants was affected at saturating light intensities. Space-grown plants showed a 25% reduction in maximum net photosynthetic rates (Fig. 1).

A decrease in photosynthesis by these C_3 leaves could occur due to an increase in photorespiration. However, these measurements were performed in 5% (v/v) CO_2, which would have minimized this process. Net photosynthetic rates also could diminish due to decreased quantum

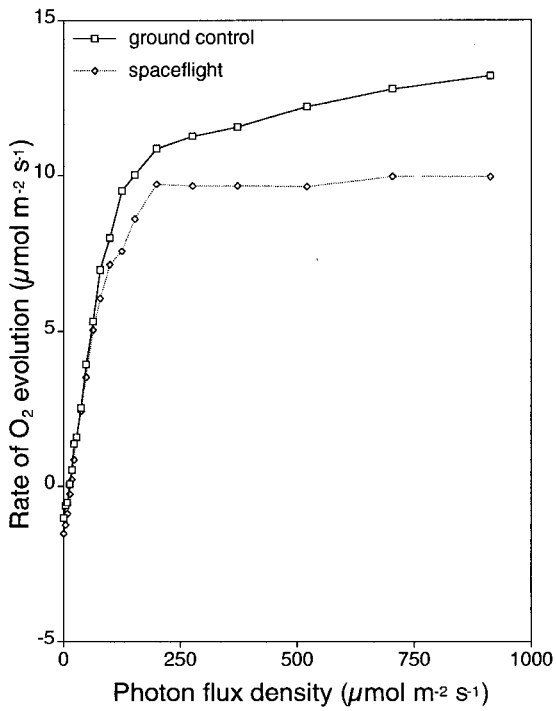

Figure 1. PPFD response curve of net O_2 evolution of leaves harvested from wheat plants grown in space or as ground controls. Photosynthetic rates were measured in 5% (v/v) CO_2 at 20°C using red-light-emitting diodes (660 nm) as the light source. The data points are the average of duplicate measurements.

yield. Therefore, the relative quantum yield of photosynthesis at limiting light intensities using red-light-emitting diodes (660 nm) as the light source was measured as the molar amount of O_2 evolved per mol of photons incident on the leaf surface. The leaves were preilluminated at low light intensity (90 μmol m^{-2} s^{-1}) to minimize the influence of the "Kok effect" on quantum yield (Kok, 1948, 1949). The relative quantum yield values of O_2 evolution by leaf discs of ground control and spaceflight samples were 0.104 ± 0.04 (quantum requirement: 9.6) and 0.101 ± 0.05 (quantum requirement: 9.9), respectively (Fig. 2). This suggests that the inherent quantum efficiency of leaves was not significantly altered by plant growth in space. The light compensation point of leaf discs of ground control plants was 12 μmol m^{-2} s^{-1} and it increased by 33% to 16 μmol m^{-2} s^{-1} in the space-grown plants. This increase in light compensation point was possibly due to the 27% increase in the dark-respiration rate of leaves of space-grown plants (increase in O_2 consumption from 1.20 μmol m^{-2} s^{-1} in ground controls to 1.53 μmol m^{-2} s^{-1} in spaceflight samples).

Electron Transport

To ascertain if the decline of light- and CO_2-saturated photosynthetic O_2 evolution in space-grown plants was due to a decrease in the light-saturated photosynthetic electron transport rates, thylakoid membranes were isolated from the leaves of ground control and spaceflight samples and the whole-chain, PSI, and PSII activities were monitored. Whole-chain electron transport measured as O_2 uptake from H_2O to MV declined by 28% in the space-grown plants relative to the ground controls (Fig. 3). Analyses of partial reactions of the electron transport chain revealed that PD-supported, PSII-dependent O_2 evolution in the space-grown samples was inhibited by 27%, and PSI-mediated electron transport measured as O_2 uptake from the exogenous electron donor $DCIPH_2$ to the electron acceptor MV was reduced by 22% relative to ground controls.

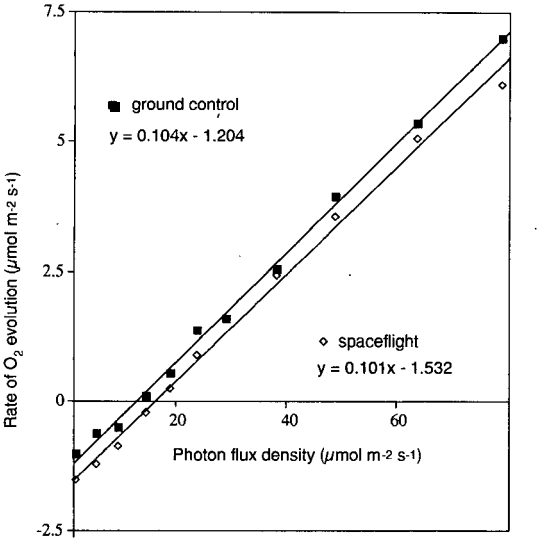

Figure 2. Relative quantum yield of net O_2 evolution by leaves harvested from wheat plants grown in space or as ground controls. Quantum yield was measured in 5% (v/v) CO_2 at limiting light intensities (0–80 μmol m^{-2} s^{-1}). Red-light-emitting diodes (660 nm) were used as the light source for quantum yield determination. Data points are the average of duplicate measurements.

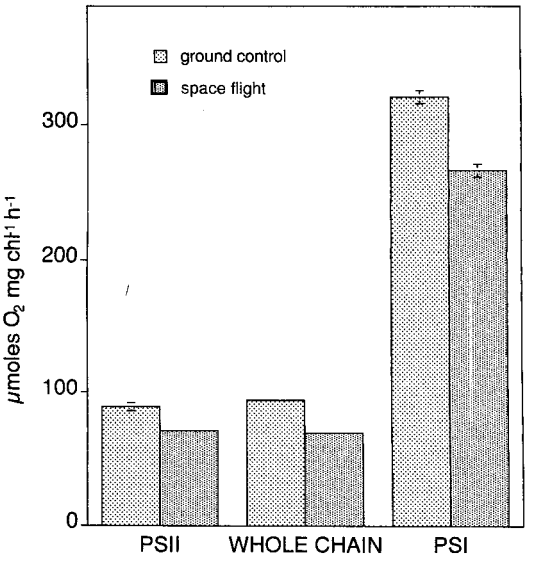

Figure 3. Photosynthetic electron transport activity of chloroplast membranes isolated from wheat leaves grown in space or as ground controls. PSII activity was measured as PD-supported O_2 evolution. The PSI reaction was measured as O_2 uptake using $DCIPH_2$ as an electron donor and MV as an electron acceptor. Whole-chain electron transport was measured as O_2 uptake having H_2O as the electron donor and MV as the electron acceptor. Data points are the average of three replicates. The error bars represent SD, and missing error bars indicate that they are smaller than the label marks.

Absorption and Fluorescence Spectra

To understand the effect of microgravity on the thylakoid membrane, room-temperature (20°C) absorption and fluorescence emission spectra of chloroplasts isolated from ground control and spaceflight samples were measured. The characteristics of the absorption spectra of thylakoids in ground control and spaceflight samples were identical (data not shown). Spaceflight samples showed a slight reduction in the room-temperature fluorescence intensity. The fluorescence emission peak, however, remained at the same position, i.e. at 683 nm for both ground control and spaceflight samples (data not shown).

DISCUSSION

In ground control samples the relative quantum yield value (0.104) of CO_2-saturated photosynthesis closely matched the value measured under identical conditions for other C_3 species (Björkman and Demmig, 1987; Walker, 1989). The relative quantum yield of space-grown plants was not significantly different. However, at saturating light intensities a 25% decrease in photosynthetic rate was observed in space-grown plants. This

inhibition of light-saturated O_2 evolution by leaf discs of space-grown wheat plants may be due to the decline (28%) in light-saturated photosynthetic whole-chain electron transport rate. Reduced photosynthetic electron transport was caused by a decrease of both PSI and PSII function in the microgravity environment. Usually, PSI is more resistant to environmental stresses such as drought, heat, and heavy metals (Hsiao, 1973; Tripathy et al., 1981, 1983). However, in microgravity PSI activity declined by roughly the same extent as that of PSII. The microgravity environment almost uniformly affected the photosynthetic electron transport chain, leading to almost identical inhibition of PSII, PSI, and whole-chain electron transport at saturating light intensity. After return of the space-grown plants to earth, the photosynthetic reactions may have recovered from the damage sustained in the microgravity environment. Therefore, postflight measurements of photosynthetic reactions may not reflect the actual degree of photosynthetic reduction in space; rather, it could be greater.

The apparent increase in dark-respiration rate (27%) in space-grown plants adds to the thermodynamic cost for their metabolic maintenance. The starch and soluble sugar content is decreased in space-grown pea, pepper, Arabidopsis, and *Lepidium* plants (Johnson and Tibbitts, 1968; Abilov et al., 1986; Laurinavichius et al., 1986; Volkmann et al., 1986; Aliyev et al., 1987; Brown et al., 1993). Although the rate of respiration has not been studied in these space-grown plants, in light of the present study with wheat, it may be inferred that reduced starch and soluble sugar contents may be partly due to their higher respiration rates in space. Similarly, the higher CO_2 level observed around space-grown sweet clover seedlings (Gallegos et al., 1994) may be due to their increased respiration in space.

The shoot fresh weight of space-grown wheat seedlings declined by 25%. This could be due partly to the increase in respiration. All plants were growing under strictly light-limiting conditions and, thus, a decline in light-saturated photosynthetic capacity would have little influence on growth rate. The quantitatively similar depressions of light-saturated photosynthetic capacity and growth rate are, therefore, likely coincidental.

The results from this study demonstrate that the CO_2- and light-saturated photosynthetic rates are affected in the spaceflight environment, which includes microgravity, low doses of cosmic radiation, and transient changes in other environmental factors. The modest decline in shoot fresh weight and photosynthetic rates of wheat plants after 10 d of growth and development in space suggests that it will be possible to produce food and biomass in space, although perhaps at a reduced rate. Both PSI and PSII rates declined at saturating light intensities in space-grown plants. Further investigations are needed to identify the causes of this decline. Once these are identified, it may be possible to overcome these problems by selecting the appropriate genotype, applying suitable genetic engineering techniques, or altering plant culture conditions.

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